**Species interactions and climate change: How the disruption of species co-occurrence will impact on an avian forest guild**

# Species interactions and climate change: how the disruption of species co-occurrence will impact on an avian forest guild

**Running Head:** Climate change and interactions in birds

Mattia Brambilla[a,b], Davide Scridel[a,c], Gaia Bazzi[b], Luca Ilahiane[b], Aaron Iemma[a], Paolo Pedrini[a], Enrico Bassi[d], Radames Bionda[e], Luigi Marchesi[a], Fulvio Genero[f], Norbert Teufelbauer[g], Remo Probst[g], Al Vrezec[h], Primož Kmecl[i], Tomaž Mihelič[i], Giuseppe Bogliani[c], Hans Schmid[j], Giacomo Assandri[a,c], Renato Pontarini[k], Veronika Braunisch[l], Raphaël Arlettaz[l], Dan Chamberlain[m]

Mattia Brambilla and Davide Scridel should be considered joint first author

[a] Museo delle Scienze, Sezione Zoologia dei Vertebrati, Trento, Italy

[b] Fondazione Lombardia per l'Ambiente, Settore biodiversità e aree protette, Seveso (MB), Italy

[c] Dipartimento di Scienze della Terra e dell'Ambiente, Università degli Studi di Pavia, Pavia, Italy

[d] Parco Nazionale dello Stelvio, Bormio (SO), Italy

[e] Parco Naturale Alpe Veglia e Devero – Alta Valle Antrona, Varzo, Italy

[f] Riserva Naturale Regionale del Lago di Cornino, Cornino (UD), Italy

[g] BirdLife Austria, Wien, Austria

[h] National Research Institute, Ljubljana, Slovenia

[i] DOPPS BirdLife Slovenia, Ljubljana, Slovenia

[j] Schweizerische Vogelwarte, Sempach, Switzerland

[k] Progetto Lince Italia, Tarvisio (UD), Italy

[l] University of Bern, Institute of Ecology and Evolution, Division of Conservation Biology, Bern, Switzerland

[m] Dipartimento di Scienze della Vita e Biologia dei Sistemi, Università di Torino, Turin, Italy

**Contact information**

corresponding author: Mattia Brambilla, phone: +39 02 80616123, email: brambilla.mattia@gmail.com

**Abstract:**

Interspecific interactions are crucial in determining species occurrence and community assembly. Understanding these interactions is thus essential for correctly predicting species' responses to climate change. We focussed on an avian forest guild of four hole-nesting species with differing sensitivities to climate, that show a range of well-understood reciprocal interactions, including facilitation, competition and predation. We modelled the potential distributions of black woodpecker and boreal, tawny and Ural owl, and tested whether the spatial patterns of the more widespread species (excluding Ural owl) were shaped by interspecific interactions. We then modelled the potential future distributions of all four species, evaluating how the predicted changes will alter the overlap between the species' ranges, and hence the spatial outcomes of interactions. Forest cover/type and climate were important determinants of habitat suitability for all species. Field data analysed with N-mixture models revealed effects of interspecific interactions on current species abundance, especially in boreal owl (positive effects of black woodpecker, negative effects of tawny owl). Climate change will impact the assemblage both at species and guild-levels, as the potential area of range-overlap, relevant for species interactions, will change in both proportion and extent in the future. Boreal owl, the most climate-sensitive species in the guild, will retreat, and the range-overlap with its main predator, tawny owl, will increase in the remaining suitable area: climate change will thus impact on boreal owl both directly and indirectly. Climate change will cause the geographical alteration or disruption of species interaction networks, with different

consequences for the species belonging to the guild and a likely spatial increase of competition and/or intraguild predation. Our work shows significant interactions and important potential changes in the overlap of areas suitable for the interacting species, which reinforce the importance of including relevant biotic interactions in predictive climate change models for increasing forecast accuracy.

**Keywords:** biotic interactions, citizen science, global warming, SDM, Strigidae, woodpeckers

## Introduction

The importance of environmental factors such as climate, topography and land-cover in dictating species distributions is well recognized in the literature (e.g. Hawkins et al., 2003; Elith & Leathwick, 2009) and it is the basis of correlative species distribution models (SDMs). These models, also known as environmental niche models (ENMs), have represented one of the most frequent applications in ecology, biogeography and conservation over recent decades (see e.g. Engler et al., 2017). In addition to the above-mentioned environmental factors, interspecific interactions can also be crucial in determining species occurrence over different spatial scales (Wisz et al., 2013), as well as in structuring biological communities (Bertness & Callaway, 1994). This underlies the growing interest in macroecological models that include or evaluate biotic interactions (Dormann et al., 2018). In fact, biotic interactions have been hypothesized from macroecological patterns (Pollock et al., 2014), as well as used to improve distribution predictions for interacting species (Araújo & Luoto, 2007; Heikkinen, Luoto, Virkkala, Pearson, & Körber, 2007).

One of the greatest recent challenges for ecologists is to predict the likely consequences of climate change on species, communities and ecosystems (Valiente-Banuet et al., 2015): proper forecasting is essential for species conservation and the maintenance of functioning ecosystems. (Groves et al., 2012). A crucial point that severely complicates the assessment of the potential impacts of climate change on wildlife is represented by its indirect effects via changes in biotic interactions (Tylianakis, Didham, Bascompte, & Wardle, 2008), to the point that considering biotic interactions is essential to correctly predict species' responses to climate change (Van der Putten, Macel, & Visser, 2010). Climate change may disrupt trophic webs by altering the distribution of species acting as key resources, competitors and predators, or by shifting phenologies of interacting organisms, ultimately causing important changes in the nature of relationships between species (Blois, Zarnetske, Fitzpatrick, & Finnegan, 2013; Kubelka et al., 2018; Van der Putten et al., 2010).

Facilitation (a positive interaction whereby one species promotes the occurrence of another) and intraguild predation are two particular biotic interactions that have been found to be very important

for predicting the occurrence of several species (Heikkinen et al., 2007; Holt & Huxel, 2007), but have received little attention in terms of how they could be altered by the influence of climate change (but see (Bateman, Vanderwal, Williams, & Johnson, 2012). In fact, variation in climatic conditions may impact on facilitation relationships as well as on intraguild predation (e.g. Rogers et al., 2018), with potentially cascading effects over the entire system (Barton & Schmitz, 2009).

In this study, we focus on an avian forest guild of four hole-nesting species with different types of reciprocal interactions, ranging from facilitation to competition and predation. The distribution of the model species we considered is partially limited by climate, and in particular by temperature. On this basis, our study system offers an unprecedented opportunity to evaluate the potential effect of climate change on species distributions and, in particular, on different types of interaction among species in the studied guild. On the basis of well-established interspecific relationships, we formulated an *a priori* interaction scenario, that accounts for the effects of co-occurrence in this guild. Then, using a large sample size and relevant environmental predictors, measured at a biologically meaningful spatial scale, we modelled potential species distributions. Successively, we evaluated whether the co-occurrence patterns that could be hypothesized on the basis of both environmental suitability (according to species-specific SDMs), and whether potential biotic interactions of the three more widespread species within the Alpine region were consistent with real occurrence data (under current climatic conditions) gathered through dedicated fieldwork. Finally, we modelled the potential future distribution of the study species according to the forecast future climate, to provide an estimate of the potential impact of climate change on (co)occurrence and hence on likely interspecific interactions.

## Material and methods

### Study system

The forest guild we investigated included four avian hole-nesting species, black woodpecker *Dryocopus martius*, boreal owl *Aegolius funereus*, tawny owl *Strix aluco* and Ural owl *Strix uralensis*. The study area encompassed the Alpine region, i.e. the Alps and the surrounding areas across seven European countries (Fig. 1). This iconic mountain system harbours all the model species, although they display rather different breeding distribution patterns. The Ural owl is limited to the eastern portion of the study area, whereas the other three species occur over most of the Alps, showing different associations with elevation belts and with forest types.

[Figure 1 approximately here]

Black woodpecker, the only diurnal taxon among the modelled species, is tied to mature forests, with large stems and availability of dead wood and ant-rich habitats (Brambilla & Saporetti, 2014; Karimi, Moradi, Rezaei, Brambilla, & Ghadimi, 2018; Pirovano & Zecca, 2014) over a wide elevation gradient, from sea level to c.2000 m asl. This species has shown a dramatic increase in the Alps, and colonization of previously unoccupied lowland forests (Nardelli et al., 2015). This expansion is most likely due to an increase in forest quality and extent (Nardelli et al., 2015; see also Mikusiński, 1995), yet no study has investigated the potential impact of climate change on this species, with the exception of a paper suggesting future retraction in central Europe (Vos et al., 2008).

The Alps are a climate *refugium* for boreal owl, representing a relict portion of the former range that the species occupied in a colder past (Brambilla et al., 2015). According to this, climate change will likely impact on boreal owl by reducing the suitability of most of its current range as a consequence of increasing temperatures (Brambilla et al., 2017; Scridel et al., 2017) and/or by altering its preferred breeding habitat type (coniferous or mixed forests) (Brambilla et al., 2015;

148 Hartl-Meier et al., 2014).

149 Tawny owl is a generalist species with a wide niche and distribution, occurring over most of
150 Europe in forest, farmland and also urban habitats, and occupying a broad climatic gradient (Francis
151 & Saurola, 2004; Vrezec & Tome, 2004a; Marchesi et al., 2006). In the Alps, the species is currently
152 expanding its distribution towards higher elevation, most likely due to milder climates (pers. obs.)
153 similar to the northwards expansion observed at higher latitudes, a response to warmer winters and
154 reduced snow cover (Francis & Saurola, 2004).

155 Ural owl, the largest of the owls studied here, is widely distributed in northern Eurasia (Konig,
156 Weick, & Becking, 1999). Towards the south it occurs mostly in mountain areas, inhabiting
157 intermediate elevations in the eastern Alps, particularly in mixed forests with mature trees and
158 clearings (Benussi & Genero, 2008; Rassati, 2006; Vrezec & Mihelič, 2013; Vrezec & Tome,
159 2004a). However, this pattern might be due to the lack of mature forest stands in the lowlands
160 because of intensive logging, since the Ural owl is relatively abundant in preserved mature forest
161 stand fragments in lowlands (Vrezec & Mihelič, 2013). Recent observations indicate that this
162 species is expanding in montane as well as in lowland forest areas in different parts of its southern
163 range in Europe (Bashta, 2009; Vrezec, 2019). So far, only a single study (Huntley, Green,
164 Collingham, & Willis, 2007) has evaluated the potential effect of climate change on its distribution
165 in central-southern Europe.

166 These four species represent an ideal set of interspecific interactions (Fig. 2) for testing the
167 potential disrupting effect of climate change. Black woodpecker facilitates the occurrence of tawny
168 and, especially, boreal owl, providing the great majority of nest cavities for the latter and potential
169 nesting sites for the former (Brambilla et al., 2013; Gustin, Brambilla, & Celada, 2010). Tawny owl
170 is one of the main predators of boreal owl (Konig et al., 1999; Mikkola, 1976). Ural owl can predate
171 both tawny and boreal owls (Mikkola, 1983); competitive exclusion of tawny owls from areas
172 occupied by Ural owls has been reported from northern (Korpimaki, 1986), southern (Vrezec &
173 Tome, 2004a) and eastern Europe (Kajtoch, Żmihorski, & Wieczorek, 2015). Even if Ural owl have

been reported to negatively affect breeding density and reproductive success of boreal owl in northern Europe (Hakkarainen & Korpimaki, 1996), the competitive exclusion exerted by Ural on tawny owl in the eastern Alps benefits the smaller boreal owl. Ural owl exerts a much lower predation pressure on boreal owl than on tawny owl, and the sites free of tawny owl created by Ural owl occurrence are regularly occupied by boreal owl (Vrezec & Tome, 2004b).

[Figure 2 approximately here]

**Data collection**

Two different datasets were used for this study. For distribution modelling, we gathered already existing, georeferenced occurrence data, fulfilling the following requirements: spatial accuracy equal or higher than 2 km, period 2000-2017, records within the breeding season of the target species (March-June), or data with an associated atlas code indicating breeding or territorial behaviour. Data were collected both via research projects and citizen science initiatives: i) during previous surveys carried out within the framework of different projects (e.g. (Brambilla et al., 2015, 2017; Mihelič et al., 2019; Vrezec & Mihelič, 2013; Vrezec & Tome, 2004a, 2004b), ii) via online platforms (www.ornitho.ch, www.ornitho.at, www.ornitho.it), after official requests specifying the aims of the study. Data were from the study area and from neighbouring sites (i.e., areas surrounding the study region, within the countries investigated; see Suppl. Mat.). A few occurrence points of black woodpecker, located at high elevations (>2000m asl) outside the breeding habitat of the species, were discarded as non representative of the environmental contexts used by the species for reproduction. The final dataset used for modelling comprised 41911 records and included the following sample sizes (number of 2km x 2km cells occupied by each species): 9323 for black woodpecker, 1207 for boreal owl, 5791 for tawny owl, and 436 for Ural owl.

The second dataset was used for testing the current effects of interspecific interactions on the

presence of three of the species, boreal owl, tawny owl and black woodpecker, given the simultaneous effects of environmental suitability and species co-occurrence. These data were collected by means of dedicated surveys, carried out in northern Italy (in Lombardy region and Trento province), during March-June 2017. Surveys consisted of point counts carried out in the morning (for black woodpecker) and on the same day at dusk/night (for owls). Points were located along several different valleys (see Fig. 1), at an average nearest neighbour distance of ~1100 m (with a minimum of ~450 m in the case of different sides of the same relief), set according to local morphology to avoid double counting of the same individuals as well as to avoid large, unsurveyed tracts of valley. However, there were some general differences in the spacing of points because of the variable geomorphology of the study sites. In Lombardy, the 122 survey sites had an average distance between neighbouring points of c. 1.3 km, and most points were separated by at least 1 km, except when placed on different sides of the same mountain massifs. Within the Trento province study sites, neighbouring points were sometimes located at closer distances (average distance ~850 m, minimum ~450), because of the complex valley morphology in the survey sites. At each point, after 10 min of listening to spontaneous vocalizations, if the target species was/were not recorded, we broadcast territorial calls (taken from Roché & Chevereau (2000) of males (owls; playback order: boreal, tawny) and drumming (woodpecker) for one minute (stopping immediately after any contacts), and listened again for four minutes. 218 points were surveyed for black woodpecker (58 once, 99 twice, 51 three times). Of these, 192 points were also surveyed for owls (57 once, 91 twice, 44 three times). The estimated position of all individuals of target species was recorded on aerial photographs or other detailed maps to avoid double counting from the same or neighbouring points. Ural owl does not occur within the test area, but there is a strong evidence base from intensive fieldwork in the eastern Alps of its interactions with the other species of the guild (Vrezec, 2019; Vrezec & Tome, 2004b, 2004a).

**Modelling current and future distributions**

To model the current and likely future distribution of the target species, we used environmental niche models, which combine the occurrence data of a species with a set of environmental predictors (including e.g. climatic, land-use/land-cover and topographical variables) to estimate the suitability of a given area for the study species. We considered a grid composed of 2 km x 2 km cells, covering the entire Alpine region. For each cell, we estimated the proportional cover of the most representative land-use/land-cover types (from CORINE CLC; European Environment Agency, 2016), tree density according to (Moreno, Neumann, & Hasenauer, 2017), and the average value for global solar radiation in May (derived from a 30-m DEM and calculated in GRASS 7.04; Neteler et al., 2012) and climatic variables (from CHELSA database; Karger et al., 2017). We then removed from the environmental predictors those occurring only rarely within the study area (identified by means of visual plotting of each predictor), and the most intercorrelated ones based on CORVIF (GVIF < 16) (Zuur, Ieno, Walker, Saveliev, & Smith, 2009); the resulting set of variables is summarised in Table S1.

We adopted a maximum entropy approach by developing MaxEnt models (Jane Elith et al., 2011; Phillips, Anderson, & Schapire, 2006) in R (R Development Core Team, 2016), using the package ENMeval (Muscarella et al., 2014). We discarded all duplicates, i.e. records occurring within a 2km x 2km cell already having a given species' record. We built models considering the effectively sampled area, by restricting background points (N = 10 000) to cells with at least one record of any of the target species. In this way, the background corresponded to the visited areas and corresponding environmental characteristics. We built models limiting the type of species-habitat relationships to linear and quadratic, to avoid overfitting; simpler models have to be preferred when it is necessary to expand model outcomes over different areas or temporal scenarios (Brambilla, Pedrini, Rolando, & Chamberlain, 2016). However, for black woodpecker, we also included hinge relationships as the simpler model was not precise enough in terms of correspondence between predicted distribution and current knowledge about real occurrence within the study region. For each species, occurrence data were partitioned into two groups, according to a checkerboard scheme

252 ("checkerboard1" in ENMeval) with each of the units aggregating four original (2km x 2km) cells.
253 This allowed testing model validity over independent datasets, assessing model robustness and
254 enhancing generalizability. Model validity was checked by evaluating variations in discriminatory
255 power (AUC – Area Under the Curve of the receiver operating characteristic (ROC) plot) over the
256 two different data partitions (bins), and by checking omission rates on test data, which had been
257 reclassified using two threshold-dependent metrics, i.e. 10% training omission rates, and training
258 omission for minimum training presence (i.e. lowest suitability at occurrence sites used for training
259 the model); omission rates larger than the expected values suggest overfitting (Muscarella et al.,
260 2014).
261 We tested different values of the regularization multiplier: each model was trained with eight
262 different values (from 0.5 to 4), and then the one with the lowest AIC was selected. Successively, all
263 variables unlikely to be important for species' distribution (i.e. with both permutation importance
264 and percentage contribution < 1) were discarded, and the model was run again with different values
265 of the regularization multiplier, until we obtained a most supported model with no variables
266 showing both permutation importance and percentage contribution < 1. The raw model outcome
267 was reclassified by means of a logistic transformation to allow an easier interpretation (Elith et al.,
268 2011). The final logistic output of the model was then reclassified into three-class maps of
269 suitability: unsuitable, partly suitable, and suitable. This reclassification was made on the basis of
270 some widely adopted thresholds, generally used for binary reclassification of MaxEnt models, i.e.
271 the $10^{th}$ percentile and the *maximum training sensitivity plus specificity threshold* (Engler, Rödder,
272 Stiels, & Förschler, 2014; Liu, Berry, Dawson, & Person, 2005; Liu, White, & Newell, 2013).
273 Values between 0 and the lowest of such thresholds were considered as unsuitable, values between
274 the thresholds as partly suitable, and values above the highest one, as definitely suitable. To
275 calculate potential range overlap between species and changes in range extent between current and
276 future conditions for each species, we considered all sites with suitability higher than the lower
277 threshold as potentially occupied by a species (thus both partly suitable and definitely suitable were

278 treated as potentially occupied). Finally, for all species, we removed all those locations at an
279 elevation higher than 2200m asl from suitable and partly suitable areas. In fact, even if some cells
280 around that elevation could be predicted as suitable for the target species, the occurrence of the
281 mature forests required by them is very unlikely at such an elevation in the Alps, and will be rather
282 unlikely to reach it in the near future.
283 Distribution models were then projected over future scenarios of climate change, derived from
284 the HADGEM model, under the worst scenario (representative concentration pathway RCP 8.5,
285 IPCC, 2013), with future climate conditions (for 2050) taken from the Worldclim database
286 (www.worldclim.org; Fick & Hijmans, 2017). We selected a single, pessimistic, scenario because i)
287 we were interested in exploring the potential effect of climate change on a guild of interacting
288 species rather than in obtaining several alternative predictions, e.g. for planning or conservation
289 purposes, and ii) scenarios with larger changes are becoming unfortunately increasingly probable
290 (Peters et al., 2013).
291
292 **Testing the effects of interspecific interactions**
293 To check whether interspecific interactions have the potential to affect the model species, we carried
294 out a field test considering current patterns of co-occurrence of three of our species in a sample of
295 sites in the Italian Alps.
296 We tested for the effect of tawny owl abundance on the number of boreal owls at survey points,
297 and of the effect of black woodpecker occurrence on the local abundance of both tawny and boreal
298 owl. N-mixture models, developed using the package 'unmarked' (Fiske & Chandler, 2011) in R (R
299 Development Core Team, 2016), were employed for evaluating the effect of species co-occurrence
300 and environmental suitability on the latent abundance of the target species, while taking into
301 account the potential variation in detectability and hence imperfect detection. Under this approach,
302 repeated counts in a set of sites are used to estimate simultaneously the detectability and the
303 abundance of individuals at survey sites (Ficetola et al., 2018; Royle, 2004). We evaluated the

304 factors that can affect the species' local density by modelling the latent abundance of each species.
305 We assumed population closure because we focused on a single breeding season.
306 As factors potentially affecting the observation process (and hence detection), we tested time of
307 day, survey date, disturbance as a three-level categorical factor (absent; weak – some far or faint
308 noises; strong – close noise or human activities potentially affecting species detection by the
309 observer or even species behaviour), and wind, a three-level categorical factor (calm - Beaufort
310 scale 0-1; weak - Beaufort scale 2-3; moderate - Beaufort scale 4-5). For boreal owl, the number of
311 calling tawny owls was also considered as a variable potentially affecting detection. Instead of
312 entering several abiotic and habitat factors potentially determining species' abundance into the
313 model, we used the environmental suitability produced by the respective MaxEnt models for each
314 species (taking the value of the model cell including the surveyed point), and the maximum
315 abundance of tawny owl recorded at a site for boreal owl. We also tested for a positive effect of
316 occurrence of black woodpecker at a survey point as a proxy for nest-site availability for both owl
317 species. All continuous variables were standardized before the analyses for a better comparison of
318 their relative effects (Cade, 2015; Schielzeth, 2010). For each species, we then developed models
319 based on all possible variable combinations, and ranked them based on the AICc (Akaike's
320 Information Criterion for small sample size), using the package 'MuMIn' (Bartoń, 2016), and
321 checked whether the co-occurrence factors were selected in the most supported models. We
322 repeated the analysis excluding the points surveyed in the Trento province, which often were closer
323 to each other, considering only the points surveyed in Lombardy (see under "Data collection") to
324 check for consistency in the model results when only well-spaced points were included.
325
326

## Results

### Current distribution and overlap

For all modelled species, the discriminatory power over the two data partitions was nearly identical (all differences < 0.013), omission rates at test sites according to the 10% training threshold showed values invariably close (0.09-0.12) to the expected one (0.10) on both bins (data partitions), and similarly omission values on both bins were always close to zero, as expected (< 0.005); most importantly, the predicted distribution matched well the known breeding range. Summary statistics for models are shown in Table S2. For Ural owl, suitable sites were predicted to occur not only within the current range of the species in the eastern Alps, but also in the central and western part of the Alpine region, although much more sparsely (Fig. 3).

[Figure 3 approximately here]

All species were associated with higher forest cover, although for boreal owl, this positive association was relevant only for coniferous forest, and for tawny owl, only deciduous forest (Table 1). Furthermore, tawny owl was negatively associated with coniferous forest. Both Ural owl and tawny owl also showed evidence of greater habitat suitability at intermediate cover of variables that can be considered as proxies for open or semi-open habitats within forests (grassland, sparsely vegetated areas, complex cultivation patterns, discontinuous urban fabric). In terms of climatic variables, there was a clearer distinction in the response of the four species. Black woodpecker exhibited a wide thermal niche, with average annual temperature from a few degrees below zero up to 15°C, whilst boreal owl inhabited a cooler part of the temperature gradient, preferring values between -2° and 5°C. Tawny owl was the only species showing a positive linear effect of average temperature on habitat suitability. Habitat suitability for Ural owl was positively affected by annual temperature range and annual precipitation, but negatively by precipitation seasonality (Table 1).

353

354 [Table 1 approximately here]

355

356 The overlap in current modelled distributions was highest for boreal owl and black woodpecker
357 (99% of the former species' range overlappig with the latter), followed by tawny and boreal owls
358 (25%), tawny and Ural owls (15%), boreal and Ural owls (12%), boreal-tawny-Ural owls (6%).

359

360 **Effect of interactions**

361 The N-mixture models revealed important effects of observation covariates on owl detection (see
362 Tables S3 and S4) and, most importantly, a positive effect of environmental suitability (as
363 calculated by MaxEnt models) on species abundance for both owl species considered in the field
364 surveys, with a particularly strong effect for tawny owl (for boreal owl, the variable ranking was
365 slightly different according to the dataset used; Tables S3 and S4). A positive effect of black
366 woodpecker occurrence was found for boreal owl, but not for tawny owl. A negative effect of the
367 abundance of tawny owl on that of boreal owl was also suggested by the models; for boreal owl, the
368 effect of variables describing interspecific interactions was particularly important (Table S3).
369 Notably, all boreal owls occurring in sites where black woodpecker was not detected during the
370 2017 survey, occupied sites predicted to be suitable for the woodpecker by the MaxEnt model, thus
371 potentially offering nest-sites excavated by the woodpecker in previous seasons. The test of
372 interaction effects therefore strongly supported the importance of interspecific interactions for
373 boreal owl, but not for tawny owl.

374

375 **Future distributions**

376 Predicted future environmental suitability for the target species is displayed in Fig. S2 and changes
377 are summarized in Table 2. The distribution of boreal owl will be substantially affected by climate
378 change, with a range reduction and especially a contraction towards higher elevation. Ural owl is

predicted to gain suitable areas in Austria and in the central and western Alps, where it is currently absent. Tawny owl will likely show a range expansion towards higher elevations, especially in the central Alps. Black woodpecker distribution will likely undergo only minor changes, even under the rather 'extreme' climate change scenario considered.

[Table 2 approximately here]

The potential overlap between the interacting species will change in the future (Fig. 4; see Table S5 for absolute variation). Almost the entire range of boreal owl is predicted to be suitable for black woodpecker both in current and future conditions (Fig. 5); the decrease in extent of potential overlap, due to owl contraction (Fig. 4 and Table S5) will not impact on the potential interactions. The predicted overlap between boreal owl and its main intraguild predator, tawny owl, will show a marked (proportional) increase (from 25% to 54% of boreal owl potential range) and, importantly, will increase in the central Alps (one of the strongholds for boreal owl under a changing climate), because milder climates will enable tawny owl to expand its potential distribution in Alpine valleys. The likely overlap between boreal and Ural owls will decrease in absolute terms, but will keep nearly stable in relative share over the boreal owl range. The areas where Ural owl occurrence could benefit boreal owl (i.e. those with potential occurrence of tawny owl) will decrease (from 6% to 2% of boreal owl range). Finally, the overlap between tawny owl and its competitor/intra-guild predator, the Ural owl, will probably increase over most of the Alps.

[Figure 4 approximately here]

[Figure 5 approximately here]

## Discussion

Modification of species interactions in terms of spatial or functional patterns is a potentially crucial, but usually overlooked, consequence of climate change on biological communities. To our knowledge, this is one of the few studies that has investigated patterns of co-occurrence for an interacting guild of birds in response to climate change. We have demonstrated the importance of these interactions on the current distribution of the focal species based on field surveys (boreal owl, tawny, black woodpecker) and empirical evidence (Ural owl). Our combined analyses indicated that both environmental variables (habitat and climate) and interactions with other species were important predictors of species occurrence. The models predicted the current species distribution well and therefore were used to evaluate the potential disruption of the interaction network (via changes in spatial co-occurrence) in this guild in response to future climatic alterations. We have shown that changes to the interaction network are likely to have highly variable effects depending on the particular species, but for boreal owl at least, a spatial increase in areas with negative interactions (without compensatory increases in areas with positive interactions) is very likely to have net negative effects in the future.

### Large-scale environmental predictors of species occurrence

Environmental correlates of habitat suitability for all model species were coherent with the biological and ecological requirements found in the literature (e.g. Lundberg, 1980; Vrezec & Bertoncelj, 2018; Vrezec & Tome, 2004b). Considering the link with climate, black woodpecker and tawny owl showed the broadest thermal niche, consistent with their wider distribution over the Palearctic. Habitat suitability for tawny owl in the Alps is linearly and positively affected by temperature and thus a positive outcome of the temperature increase could be expected for that species. The recent increase of tawny owl at higher elevations observed in several sites in the Alps (all authors, pers. obs.) confirms this pattern. While temperature changes in the Alpine region are unlikely to severely impact black woodpecker and Ural owl, a strong effect could be expected for

boreal owl. For the woodpecker, a possible minor shift towards upper elevations could be expected under extreme scenarios, which is consistent with the broader distribution of the species, which is much more abundant in mountain areas in southern Europe. Boreal owl has already been reported as a climate-sensitive species in the Alps (Brambilla et al., 2015), its distribution at the European scale appears strictly related to temperature (Brambilla et al., 2017), and it is among the cold-adapted species undergoing population decline and range contraction in Europe (Korpimaki & Hakkarainen, 2012) and Italy (Scridel et al., 2017).

**Interspecific interactions, climate change and its consequences**

The relative abundance of boreal owl at sampling sites revealed the potential importance of co-occurrence patterns on the species' distribution. Black woodpecker occurrence and abundance of tawny owl were indeed even more important than environmental suitability *per se* for boreal owl in the Central Italian Alps (see under 'Modelling issues' for further discussion), and likely also in the wider Alpine region (Vrezec & Tome, 2004b). This means that, within this largely suitable belt, interspecific dynamics play an important role in driving the occurrence of boreal owl, the species most sensitive to interactions of those investigated. For tawny owl, the presence of black woodpecker is less relevant as the former species has a greater flexibility in selecting suitable cavities for breeding, which include woodpecker holes, but also a variety of old nests, rotten tree trunks, other holes, ledges in rock cliffs and even buildings (Mikkola, 1983). For tawny owl, the environmental suitability derived from MaxEnt models was a better predictor of abundance.

**Changes in the predicted 'room for interactions'**

According to our analysis, climate change will strongly impact on the investigated species both at species level and in the form of community changes in interacting species resulting from distribution shifts, as the area where species interactions are likely to occur is predicted to vary in extent in the future. In most cases, the potential overlap between species range will decline, but it

will likely increase for tawny owl and Ural owl, potentially increasing the frequency of competitive interactions between the species. The spatial relevance of the facilitator role of black woodpecker in favour of boreal owl will probably remain unchanged.

Boreal owl was the most climate-sensitive species, and will retreat further into the mountains. For this reason alone, the species will lose 65% of its habitat. Therefore, it is not surprising that, while the absolute overlap with the tawny owl will decrease (-26%), the overlap will increase in the area remaining suitable for boreal owl (from 25% to 54%). Since the potential overlap with the black woodpecker and the Ural owl will remain roughly the same, climate change will have a negative effect on the boreal owl both directly (via contraction of suitable areas) and indirectly, via a likely increase in the overlap with tawny owl.

Interestingly, our modelling outcomes suggested a potential westwards expansion of Ural owl. This species was until recently confined to the very eastern side of the Alps and eastern Europe (Vrezec, 2009), but was more westerly distributed in historical times (Goffette, Denis, Pöllath, & van Neer, 2016) and in recent decades it has colonized new areas, expanding its range towards the central portion of the Alpine chain (Benussi & Genero, 2008, 2017; Nardelli et al., 2015; Rassati, 2006, 2017). Therefore, the modelled increase in suitability in the central and western Alps is fully coherent with the current pattern of range expansion. Successful reintroduction projects recently carried out in Lower Austria (Zink & Walter, 2018) further confirm environmental suitability of the central-eastern Alps for the species, where the provisioning of nest-boxes, which compensates for the widespread lack of nesting sites due to forest harvesting, could further favour the species' westward expansion. The ongoing expansion of Ural owl, coupled with that of tawny owl, implies an increasing potential overlap and thus likely increasing interactions between these two competing species (Figs. 4 and 5).

**Modelling issues**

The distribution models we obtained (at a spatial scale highly representative of the territory

size/home range of the species) appeared rather robust for all species, with a high level of consistency in discriminatory power over the two partitions of the dataset (Table S2). The resulting predicted distributions were in line with the current range of target species in the Alps. Similarly, the species-habitat relationships underlying the models were coherent with the knowledge of species' ecology.

Other species interact with the target ones. These basically include prey, and especially voles (Brommer, Pietiäinen, & Kolunen, 2002; Korpimaki & Hakkarainen, 2012; Vrezec, Saurola, Avotins, Kocijančič, & Sulkava, 2018), as well as other predators, like goshawk *Accipiter gentilis* and eagle owl *Bubo bubo* (Byholm, Burgas, Virtanen, & Valkama, 2012; Hakkarainen & Korpimaki, 1996; Lõhmus, 2003; Mikkola, 1976, 1983; Sergio, Marchesi, Pedrini, & Penteriani, 2007). Such additional factors might further modulate the effect of competition and coexistence at a finer scale (Ciach, 2008; Ciach & Czyżowicz, 2014).

Finally, local forest characteristics, potentially sensitive to human management and climate change (Braunisch et al., 2014), can be important, especially for black woodpecker (Karimi et al., 2018; Pirovano & Zecca, 2014). However, at broader scales they are unlikely to be relevant (see e.g. Tjernberg, Johnsson, & Nilsson, 1993; Brambilla & Saporetti, 2014), as the ongoing range expansion in a large part of the study area suggests (Gustin, Brambilla, & Celada, 2019). In addition, we cannot completely exclude the possibility that the effect of black woodpecker and tawny owl (positive and negative, respectively) on boreal owl occurrence, highlighted by N-mixture models, could be due to an influence of some unmeasured habitat variable which has an effect on both interacting species of a given species pair. However, we are confident that these effects are likely mirroring true interaction effects. Black woodpeckers provide almost all boreal owl nest-sites in the study area (Pedrini, Caldonazzi, & Zanghellini, 2005), and hence a potential unmeasured habitat variable could also be represented by a better-than-average availability of cavities. On the other side, tawny owls have been shown to significantly impact on boreal owl occurrence (Vrezec & Tome, 2004b), and we are aware of several cases of local replacement in recent years (our pers. obs.

509 from Italy, Austria and Slovenia). Nevertheless, long-term studies that include more detailed habitat
510 descriptions would better elucidate whether the positive and negative relationships are consistent
511 with regard to temporal variation in the same habitat, and therefore some caution is needed in
512 interpreting the observed patterns.
513
514 **Conclusions**
515 Climate change will result in the disruption or alteration of species interaction networks (Blois et
516 al., 2013; Tylianakis et al., 2008). Several studies have investigated the potential impacts of
517 variations in climate on animal-plant networks (insects and host species, plants and their pollinators;
518 e.g. Schweiger et al., 2008; Gorostiague et al., 2018). However, fewer studies have dealt with
519 changes in interspecific relationships among vertebrates, with the main exception represented by
520 carnivorous mammals (e.g. Zielinski et al., 2017; Pandey & Papeş, 2018; Scully et al., 2018). Here,
521 we have shown how climate change will result in changes in the distribution overlap in a guild of
522 interacting species, with different consequences for the species belonging to this guild. The process
523 will likely result in an increase in areas were the target species will experience competition and/or
524 intraguild predation rates, due to a higher proportional range overlap between subordinate (boreal
525 and tawny owl) and dominant (tawny and Ural owl, respectively) species. In turn, these changes
526 will probably enhance the importance of interaction effects for those species at the regional scale.
527 The facilitation provided by black woodpecker to boreal owl (nest provision) would instead remain
528 substantially unchanged, but the latter species will likely be the most negatively affected by climate
529 change.
530 Our work modelled the potential effects of climate change on the distribution of an interacting
531 owl guild and of its main nest facilitator, the black woodpecker, and showed potential important
532 changes in the overlap of suitable areas for those interacting species. The analysis of current
533 patterns of abundance at the local scale confirmed the likely importance of interspecific
534 interactions. Taken together, our findings suggest that future predictions of species distribution

under climate change should include relevant biotic interactions to achieve higher forecast accuracy; in particular, testing the relevance of interspecific interactions will facilitate the interpretation of distribution models and the more reliable estimation of predicted range changes.

**Acknowledgements**

Swiss data were archived in www.ornitho.ch and provided by the Swiss Ornithological Institute. Austrian data were archived in www.ornitho.at and provided by BirdLife Austria. Slovenian data were in the most part archived in www.ptice.si/noags and provided by DOPPS BirdLife Slovenia. Italian data were partly provided by www.ornitho.it. Data from Piedmont were partly provided by GPSO; data from Trentino were largely provided by the MUSE/PAT webGIS developed under the project LIFE+ TEN. We are very grateful to Fabrizio Florit, ASTORE FVG (board council and members), Matteo de Luca, Matteo Skodler, Alessandro Bertoli, Enrico Benussi, Matteo Toller, Adamo Moreno, and Regione Friuli-Venezia Giulia for providing data from this region. We are grateful to Matteo Anderle, Alessandro Franzoi, Andrea Parisi, Piergiovanni Partel, Diego Rubolini, Roberto Lardelli, and to all observers contributing data to the online platforms www.ornitho.at, www.ornitho.ch, www.ornitho.it, www.ptice.si/noags. We are also very grateful to an anonymous reviewer for helpful comments on a first draft of the manuscript. MB, GBa and LI were partly supported by the project LIFE+ GESTIRE2020. Fieldwork in Trentino was partly supported under provincial RDP fundings. Parco Naturale Paneveggio-Pale di San Martino partly supported this research as part of DS's PhD. AV was supported by research core funding No. P1-0255 by the Slovenian Research Agency.

**Author contributions**

MB conceived the idea, which was then developed by all authors. MB, DS, PP, GBa, LI, EB, RB,

LM, FG, NT, RP, AV, PK, TM, RP, GA, HS collected data on the field and/or through database interrogation. DS processed bird data; DS and AI prepared environmental layers. MB ran the analyses and all authors contributed to model checking/development and check final model outcomes. MB with DS' help wrote a first draft of the ms. All authors critically contributed to the final version.

567 **Table 1.** Environmental factors used to model species distributions that were selected in at least one
568 model (see Table S1 for full list), the relative importance of each factor (percentage
569 contribution/permutation importance) and short description of the effect (within brackets; relative to
570 the model including all the selected predictors) according to final models for each species.
571 Numerical codes for land cover variables represent CORINE categories. Symbols used for effects:
572 +: positive, -: negative, +/-: quadratic (hump-shaped), -/++: quadratic (U-shaped), +/--: quadratic
573 (hump-shaped)/negative, 0: nearly null (very weak positive effect).
574

| Variable | Description | Boreal owl | Tawny owl | Ural owl | Black woodpecker |
|---|---|---|---|---|---|
| bio_1 | Annual Mean Temperature | 76.60/81.27 (+/--) | 31.93/54.68 (+) | | 16.91/20.23 (+/--) |
| bio_12 | Annual Precipitation | | 1.47/2.67 (+) | 17.61/2.80 (+) | 14.17/36.82 (-) |
| bio_15 | Precipitation Seasonality (Coefficient of Variation) | 2.96/4.21 (-) | 5.93/0.00 (-) | 12.47/22.94 (-) | |
| bio_19 | Precipitation of Coldest Quarter | 2.64/0.37 (-/+) | | 4.05/0.00 (0) | |
| bio_7 | Temperature Annual Range (BIO5-BIO6) | 2.23/5.66 (-) | 24.01/35.13 (-) | 15.99/14.94 (+) | |
| solarMay | Global solar radiation for May | | 1.66/4.49 (+) | 0.86/0.78 (+) | 8.24/13.22 (+/--) |
| X15 | 2.2.1 Vineyards | | | | 0.64/0.66 (-) |
| X18 | 2.3.1 Pastures | | 1.02/0.43 (+) | 0.61/0.22 (-) | 0.20/0.69 (-) |
| X1.1 | 1.1.2 Continuous urban fabric | | | 0.38/0.94 (+) | 0.90/0.25 (-) |
| X2.1 | 1.1.1 Discontinuous urban fabric | 0.29/1.05 (-) | 0.85/0.77 (+) | 1.03/0.94 (+) | 1.60/0.0 (-) |
| X20 | 2.4.2 Complex cultivation patterns | | 0.25/1.21 (+) | | 0.65/3.33 (-) |
| X21 | 2.4.3 Land principally occupied by agriculture, with significant areas of natural vegetation | | | 0.62/0.42 (-) | |
| X25 | 3.1.3 Mixed forest | | | 4.75/0.00 (+) | |
| X26 | 3.2.1 Natural grasslands | | 9.44/0.00 (-) | | |
| X31 | 3.3.2 Bare rocks | | 2.79/0.44 (-) | | |
| X32 | 3.3.3 Sparsely vegetated areas | 0.75/0.48 (-) | 6.03/0.00 (-) | 1.55/1.50 (-) | |
| X35 | 4.1.1 Inland marshes | | | | 1.61/2.97 (+) |
| X4 | 1.2.2 Road and rail networks and associated land | | | | 0.49/2.31 (-) |
| X40 | 5.1.1 Water courses | | | | 1.03/3.43 (+) |
| x2632_TCD_TCD_20m | Tree cover density | 0.72/1.63 (+) | | 25.89/0.22 (-) | 18.07/11.02 (+/-) |
| X2.2 | x2632_TCD_FTY_20m Coniferous forest | 13.83/5.33 (+) | 14.62/0.19 (-) | 5.16/17.55 (+) | 33.63/2.00 (+) |

| | | | |
|---|---|---|---|
| X1.2 | x2632_TCD_FTY_20m Deciduous forest | 9.14/36.75 (+) | 1.84/3.07 (+) |

575

576 **Table 2.** Predicted extent of suitable habitats in current and future conditions (RCP 8.5 scenario for

577 2050) for the target species.

578

| **Species** | **current extent of suitable area (km$^2$)** | **future extent of suitable area (km$^2$)** | **change (%)** |
|---|---|---|---|
| boreal owl | 85644 | 29988 | -65 |
| tawny owl | 95200 | 120928 | +27 |
| Ural owl | 20012 | 67200 | +236 |
| black woodpecker | 160452 | 151564 | -6 |

579

580

581

582

583 **Figure captions**

584

585 **Figure 1.** Study area. The darker the colour, the higher the elevation. The inset shows the location
586 of the point counts (yellow dots) used to test the interspecific effects on current distribution patterns
587 for boreal and tawny owl.

588

589 **Figure 2.** Schematic representation of the interspecific interactions characterizing the study guild of
590 forest birds. Larger arrows indicate stronger effects. The negative effect of Ural owl on tawny owl,
591 in combination with the negative effect of tawny owl on boreal owl, appears as facilitation for
592 boreal owl when viewed in isolation.

593

594 **Figure 3.** Modelled current distribution or boreal owl (upper left), tawny owl (upper right), Ural
595 owl (lower left) and black woodpecker (lower right). The darker the colour, the higher the
596 environmental suitability.

597

598 **Figure 4.** Predicted range overlap under current (yellow) and future climatic conditions (blue; in
599 green, areas with predicted overlap under both scenarios), between boreal owl and black
600 woodpecker (upper left), boreal owl and tawny owl (upper right), tawny owl and Ural owl (lower
601 left), boreal owl and Ural owl (lower right).

602

603 **Figure 5.** Graphical representation of predicted extent of overlap between species and relative
604 variation due to climate change. For each scenario (current and future), boreal owl range is depicted
605 in beige, and tawny owl range in brown. The proportional overlap with other species is shown in
606 each pie chart, in black (black woodpecker for boreal owl), brown (tawny owl for boreal owl), grey
607 (Ural owl for both species). For boreal owl, the overlap with both tawny and Ural owl is shown in
608 grey-brown. Pie chart size is proportional to the relative value of current (100%) and future species

609 range (35% for boreal owl, 127% for tawny owl).

610

## References

612 Araújo, M. B., & Luoto, M. (2007). The importance of biotic interactions for modelling
613 species distributions under climate change. *Global Ecology and Biogeography*, *16*(6),
614 743–753. https://doi.org/10.1111/j.1466-8238.2007.00359.x

615 Barton, B. T., & Schmitz, O. J. (2009). Experimental warming transforms multiple predator
616 effects in a grassland food web. *Ecology Letters*, *12*(12), 1317–1325.
617 https://doi.org/10.1111/j.1461-0248.2009.01386.x

618 Bartoń, K. (2016). *MuMIn: Multi-Model Inference. R package version 1.15.6*. Retrieved from
619 https://cran.r-project.org/web/packages/MuMIn/index.html

620 Bashta, A.-T. (2009). Ural Owl Strix uralensis Population Dynamics and Range Expansion in
621 Western Ukraine. *Ardea*, *97*(4), 483–487. https://doi.org/10.5253/078.097.0412

622 Bateman, B. L., Vanderwal, J., Williams, S. E., & Johnson, C. N. (2012). Biotic interactions
623 influence the projected distribution of a specialist mammal under climate change.
624 *Diversity and Distributions*, *18*(9), 861–872. https://doi.org/10.1111/j.1472-
625 4642.2012.00922.x

626 Benussi, E., & Genero, F. (2008). Allocco degli Urali Strix uralensis: nidificazione in
627 cassetta-nido e aggiornamento della distribuzione in Italia. *Quaderni Di Birdwatching*,
628 *10*, https://www.ebnitalia.it/Qb/QB020/allocco_ur.htm. Retrieved from
629 https://www.ebnitalia.it/Qb/QB020/allocco_ur.htm

630 Benussi, E., & Genero, F. (2017). Nuovi dati sulla distribuzione e nidificazione di allocco
631 degli Urali Strix uralensis nel Tarvisiano (Alpi orientali). In S. G. Fasano & D. Rubolini
632 (Eds.), *Riassunti del XIX Convegno Italiano di Ornitologia. Torino, 27 settembre - 1*
633 *ottobre 2017* (pp. 28–29). Torino: Tichodroma. Monografie del Gruppo Piemontese Studi
634 Ornitologici.

635 Bertness, M. D., & Callaway, R. (1994). Positive interactions in communities. *Trends in*
636 *Ecology and Evolution*, *9*(5), 191–193. https://doi.org/10.1016/0169-5347(94)90088-4

637 Blois, J. L., Zarnetske, P. L., Fitzpatrick, M. C., & Finnegan, S. (2013). Climate change and
638 the past, present, and future of biotic interactions. *Science*, Vol. 341, pp. 499–504.
639 https://doi.org/10.1126/science.1237184

640 Brambilla, M., Bassi, E., Bergero, V., Casale, F., Chemollo, M., Falco, R., … Vitulano, S.
641 (2013). Modelling distribution and potential overlap between Boreal Owl Aegolius
642 funereus and Black Woodpecker Dryocopus martius: implications for management and
643 monitoring plans. *Bird Conservation International*, *23*(04), 502–511.
644 https://doi.org/10.1017/S0959270913000117

645 Brambilla, M., Bergero, V., Bassi, E., & Falco, R. (2015). Current and future effectiveness of
646 Natura 2000 network in the central Alps for the conservation of mountain forest owl
647 species in a warming climate. *European Journal of Wildlife Research*, *61*(1), 35–44.
648 https://doi.org/10.1007/s10344-014-0864-6

649 Brambilla, M., Caprio, E., Assandri, G., Scridel, D., Bassi, E., Bionda, R., … Chamberlain, D.

(2017). A spatially explicit definition of conservation priorities according to population resistance and resilience, species importance and level of threat in a changing climate. *Diversity and Distributions*, *23*(7), 727–738. https://doi.org/10.1111/ddi.12572

Brambilla, M., Pedrini, P., Rolando, A., & Chamberlain, D. E. (2016). Climate change will increase the potential conflict between skiing and high-elevation bird species in the Alps. *Journal of Biogeography*, *43*(11), 2299–2309. https://doi.org/10.1111/jbi.12796

Brambilla, M., & Saporetti, F. (2014). Modelling distribution of habitats required for different uses by the same species: Implications for conservation at the regional scale. *Biological Conservation*, *174*, 39–46. https://doi.org/10.1016/j.biocon.2014.03.018

Braunisch, V., Coppes, J., Arlettaz, R., Suchant, R., Zellweger, F., & Bollmann, K. (2014). Temperate Mountain Forest Biodiversity under Climate Change: Compensating Negative Effects by Increasing Structural Complexity. *PLoS ONE*, *9*(5), e97718. https://doi.org/10.1371/journal.pone.0097718

Brommer, J. E., Pietiäinen, H., & Kolunen, H. (2002). Reproduction and Survival in a Variable Environment: Ural Owls (Strix Uralensis) and the Three-Year Vole Cycle. *The Auk: Ornithological Advances*, *119*(2), 544–550. https://doi.org/10.1642/0004-8038(2002)119[0544:rasiav]2.0.co;2

Byholm, P., Burgas, D., Virtanen, T., & Valkama, J. (2012). Competitive exclusion within the predator community influences the distribution of a threatened prey species. In *Ecology* (Vol. 93). Retrieved from https://esajournals.onlinelibrary.wiley.com/doi/pdf/10.1890/12-0285.1

Cade, B. S. (2015). Model averaging and muddled multimodel inferences. *Ecology*, *96*(9), 2370–2382. https://doi.org/10.1890/14-1639.1

Ciach, M. (2008). Abundance and distribution patterns of owls in Pieniny National Park, Southern Poland. *Acta Zoologica Cracoviensia*, *48*(1), 21–33. https://doi.org/10.3409/173491505783995680

Ciach, M., & Czyżowicz, S. (2014). Abundance and distribution of owls Strigiformes in the Pieniny Mountains National Park (southern Poland)-the pattern of changes in the protected area after 10 years. In *Ornis Polonica* (Vol. 55). Retrieved from http://www.ornis-polonica.pl/_pdf/OP_2014_2_083-095.pdf

Dormann, C. F., Bobrowski, M., Dehling, D. M., Harris, D. J., Hartig, F., Lischke, H., … Kraan, C. (2018). Biotic interactions in species distribution modelling: 10 questions to guide interpretation and avoid false conclusions. *Global Ecology and Biogeography*. https://doi.org/10.1111/geb.12759

Elith, J, & Leathwick, J. (2009). Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution,*. Retrieved from http://www.annualreviews.org/eprint/HWR4cusJrXYCSPZ9sUDj/full

Elith, Jane, Phillips, S. J., Hastie, T., Dudík, M., Chee, Y. E., & Yates, C. J. (2011). A

statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*, *17*(1), 43–57. https://doi.org/10.1111/j.1472-4642.2010.00725.x

Engler, J. O., Rödder, D., Stiels, D., & Förschler, M. I. (2014). Suitable, reachable but not colonised: seasonal niche duality in an endemic mountainous songbird. *Journal of Ornithology*, *155*(3), 657–669. https://doi.org/10.1007/s10336-014-1049-5

Engler, J. O., Stiels, D., Schidelko, K., Strubbe, D., Quillfeldt, P., & Brambilla, M. (2017). Avian SDMs: current state, challenges, and opportunities. *Journal of Avian Biology*, Vol. 48, pp. 1483–1504. https://doi.org/10.1111/jav.01248

European Environment Agency. (2016). Corine Land Cover 2012. Retrieved from https://www.eea.europa.eu/data-and-maps/data/external/corine-land-cover-2012 website: https://www.eea.europa.eu/data-and-maps/data/external/corine-land-cover-2012

Ficetola, G. F., Barzaghi, B., Melotto, A., Muraro, M., Lunghi, E., Canedoli, C., … Manenti, R. (2018). N-mixture models reliably estimate the abundance of small vertebrates. *Scientific Reports*, *8*(1). https://doi.org/10.1038/s41598-018-28432-8

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*. https://doi.org/10.1002/joc.5086

Fiske, I. J., & Chandler, R. B. (2011). unmarked : An R Package for Fitting Hierarchical Models of Wildlife Occurrence and Abundance. *Journal of Statistical Software*, *43*(10), 1–23. https://doi.org/10.18637/jss.v043.i10

Francis, C. M., & Saurola, P. (2004). Estimating components of variance in demographic parameters of Tawny Owls, Strix aluco. *Animal Biodiversity and Conservation*, *27*(1), 489–502. https://doi.org/57354

Goffette, Q., Denis, M., Pöllath, N., & van Neer, W. (2016). Change in historical range of the ural owl in Europe. *Belgian Journal of Zoology*, *146*(1), 33–43.

Gorostiague, P., Sajama, J., & Ortega-Baes, P. (2018). Will climate change cause spatial mismatch between plants and their pollinators? A test using Andean cactus species. *Biological Conservation*, *226*, 247–255. https://doi.org/10.1016/j.biocon.2018.07.003

Groves, C. R., Game, E. T., Anderson, M. G., Cross, M., Enquist, C., Ferdaña, Z., … Shafer, S. L. (2012). Incorporating climate change into systematic conservation planning. *Biodiversity and Conservation*, *21*(7), 1651–1671. https://doi.org/10.1007/s10531-012-0269-3

Gustin, M., Brambilla, M., & Celada, C. (2010). *Valutazione dello Stato di Conservazione dell'avifauna italiana. Volume I. Non Passeriformes.* Ministero dell'Ambiente e della Tutela del Territorio e del Mare, Lega Italiana Protezione Uccelli (LIPU).

Gustin, M., Brambilla, M., & Celada, C. (2019). *Conoscerli, proteggerli. Guida allo stato di Conservazione degli uccelli in Italia*. Parma: LIPU/BirdLife Italia.

725 Hakkarainen, H., & Korpimaki, E. (1996). Competitive and Predatory Interactions among
726 Raptors: An Observational and Experimental Study. *Ecology*, *77*(4), 1134–1142.
727 https://doi.org/10.2307/2265582

728 Hartl-Meier, C., Zang, C., Dittmar, C., Esper, J., Göttlein, A., & Rothe, A. (2014).
729 Vulnerability of Norway spruce to climate change in mountain forests of the European
730 Alps. *Climate Research*, *60*(2), 119–132. https://doi.org/10.3354/cr01226

731 Hawkins, B. A., Field, R., Cornell, H. V., Currie, D. J., Guégan, J.-F. F., Kaufman, D. M., …
732 Turner, J. R. G. (2003). Energy, water, and broad-scale geographic patterns of species
733 richness. *Ecology*, *84*(12), 3105–3117. https://doi.org/10.1890/03-8006

734 Heikkinen, R. K., Luoto, M., Virkkala, R., Pearson, R. G., & Körber, J. (2007). Biotic
735 interactions improve prediction of boreal bird distributions at macro-scales. *Global*
736 *Ecology and Biogeography*, *16*(6), 754–763. https://doi.org/10.1111/J.1466-
737 8238.2007.00345.X

738 Holt, R. D., & Huxel, G. R. (2007). Alternative prey and the dynamics of intraguild predation:
739 Theoretical perspectives. *Ecology*, *88*(11), 2706–2712. https://doi.org/10.1890/06-1525.1

740 Huntley, B., Green, R. E., Collingham, Y. C., & Willis, S. G. (2007). A climatic atlas of
741 European breeding birds. In *A climatic atlas of European breeding birds*.

742 IPCC. (2013). Working Group I Contribution to the IPCC Fifth Assessment Report, Climate
743 Change 2013: The Physical Science Basis. In *Ipcc* (Vol. AR5).
744 https://doi.org/10.1017/CBO9781107415324.Summary

745 Kajtoch, Ł., Żmihorski, M., & Wieczorek, P. (2015). Habitat displacement effect between two
746 competing owl species in fragmented forests. *Population Ecology*, *57*(3), 517–527.
747 https://doi.org/10.1007/s10144-015-0497-y

748 Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., … Kessler,
749 M. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific*
750 *Data*, *4*, 170122. https://doi.org/10.1038/sdata.2017.122

751 Karimi, S., Moradi, H. V., Rezaei, H. R., Brambilla, M., & Ghadimi, M. (2018). Fine-scale
752 habitat use by black woodpecker Dryocopus martius: A year-round study in the
753 Hyrcanian forest, Iran. *North-Western Journal of Zoology*, *14*(1), 76–84.

754 Konig, C., Weick, F., & Becking, J. H. (1999). *Owls, a guide to the owls of the world*. Sussex:
755 Pica Press.

756 Korpimaki, E. (1986). Niche Relationships and Life-History Tactics of Three Sympatric Strix
757 Owl Species in Finland. *Ornis Scandinavica*, *17*(2), 126–132.
758 https://doi.org/10.2307/3676861

759 Korpimaki, E., & Hakkarainen, H. (2012). The Boreal Owl. In *The Boreal Owl*.
760 https://doi.org/10.1017/cbo9780511844164

761 Kubelka, V., Šálek, M., Tomkovich, P., Végvári, Z., Freckleton, R. P., & Székely, T. (2018).

762 Global pattern of nest predation is disrupted by climate change in shorebirds. *Science*
763 *(New York, N.Y.)*, *362*(6415), 680–683. https://doi.org/10.1126/science.aat8695

764 Liu, C., Berry, P. M., Dawson, T. P., & Person, R. G. (2005). Selecting Thresholds of
765 Occurrence in the Predictions of Species Distribution. *Ecography*, *28*(3), 385–393.
766 Retrieved from http://onlinelibrary.wiley.com/doi/10.1111/j.0906-7590.2005.03957.x/full

767 Liu, C., White, M., & Newell, G. (2013). Selecting thresholds for the prediction of species
768 occurrence with presence-only data. *Journal of Biogeography*, *40*(4).
769 https://doi.org/10.1111/jbi.12058

770 Lõhmus, A. (2003). Do Ural owls (Strix uralensis) suffer from the lack of nest sites in
771 managed forests? *Biological Conservation*, *110*(1), 1–9. https://doi.org/10.1016/S0006-
772 3207(02)00167-2

773 Lundberg, A. (1980). Why Are the Ural Owl Strix uralensis and the Tawny Owl S. aluco
774 Parapatric in Scandinavia? *Ornis Scandinavica*, *11*(2), 116.
775 https://doi.org/10.2307/3675917

776 Marchesi, L., Sergio, F., & Pedrini, P. (2006). Implications of temporal changes in forest
777 dynamics on density, nest-site selection, diet and productivity of Tawny Owls Strix aluco
778 in the Alps. *Bird Study*, *53*(3), 310–318. https://doi.org/10.1080/00063650609461447

779 Mihelič, T., Kmecl, P., Denac, K., Koce, U., Vrezec, A., & Denac, D. (2019). *Atlas ptic*
780 *Slovenije. Popis gnezdilk 2002-2017* (T. Mihelič, P. Kmecl, K. Denac, U. Koce, A.
781 Vrezec, & D. Denac, Eds.). Ljubljana: DOPPS.

782 Mikkola, H. (1976). Owls killing and killed by other owls and raptors in Europe. *British*
783 *Birds*, *69*(April), 144–154.

784 Mikkola, H. (1983). Owls of Europe. *A.D. & T. Poyser, Calton*, 397.
785 https://doi.org/10.1111/j.1467-8691.2007.00421.x

786 Mikusiński, G. (1995). Population trends in black woodpecker in relation to changes and
787 characteristics of European forests. *Ecography*, *18*(4), 363–369.
788 https://doi.org/10.1111/j.1600-0587.1995.tb00139.x

789 Moreno, A., Neumann, M., & Hasenauer, H. (2017). Forest structures across Europe.
790 *Geoscience Data Journal*, *4*(1), 17–28. https://doi.org/10.1002/gdj3.45

791 Muscarella, R., Galante, P. J., Soley-Guardia, M., Boria, R. A., Kass, J. M., Uriarte, M., &
792 Anderson, R. P. (2014). ENMeval: An R package for conducting spatially independent
793 evaluations and estimating optimal model complexity for <scp>Maxent</scp> ecological
794 niche models. *Methods in Ecology and Evolution*, *5*(11), 1198–1205.
795 https://doi.org/10.1111/2041-210X.12261

796 Nardelli, R., Andreotti, A., Bianchi, E., Brambilla, M., Brecciaroli, B., Celada, C., … Serra, L.
797 (2015). *Rapporto sull'applicazione della Direttiva 147/2009/CE in Italia: dimensione,*
798 *distribuzione e trend delle popolazioni di uccelli (2008-2013)*. Rome: ISPRA, Serie
799 Rapporti, 219/2015.

Neteler, M., Bowman, M. H., Landa, M., & Metz, M. (2012). GRASS GIS: A multi-purpose open source GIS. *Environmental Modelling & Software*, *31*, 124–130. https://doi.org/10.1016/j.envsoft.2011.11.014

Pandey, R., & Papeş, M. (2018). Changes in future potential distributions of apex predator and mesopredator mammals in North America. *Regional Environmental Change*, *18*(4), 1223–1233. https://doi.org/10.1007/s10113-017-1265-7

Pedrini, P., Caldonazzi, M., & Zanghellini, S. (2005). Atlante degli Uccelli nidificanti e svernanti in provincia di Trento. *Studi Trentini Di Scienze Naturali, Acta Biologica*, *80*, suppl. 2.

Peters, G. P., Andrew, R. M., Boden, T., Canadell, J. G., Ciais, P., Le Quéré, C., … Wilson, C. (2013). The challenge to keep global warming below 2C. *Nature Climate Change*, *3*(1), 4–6. https://doi.org/10.1038/nclimate1783

Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, *190*(3), 231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026

Pirovano, A. R., & Zecca, G. (2014). Black woodpecker dryocopus martius habitat selection in the italian alps: Implications for conservation in Natura 2000 network. *Bird Conservation International*, Vol. 24, pp. 299–315. https://doi.org/10.1017/S0959270913000439

Pollock, L. J., Tingley, R., Morris, W. K., Golding, N., O'Hara, R. B., Parris, K. M., … Mccarthy, M. A. (2014). Understanding co-occurrence by modelling species simultaneously with a Joint Species Distribution Model (JSDM). *Methods in Ecology and Evolution*, *5*(5). https://doi.org/10.1111/2041-210X.12180

R Development Core Team. (2016). *A Language and Environment for Statistical Computing*. Retrieved from https://www.r-project.org

Rassati, G. (2006). Primi dati su presenza, svernamento e nidificazione dell'Allocco degli Urali Strix uralensis nel Friuli settentrionale (Alpi orientali). *Picus*, *32*, 1–3.

Rassati, G. (2017). Allocco degli Urali Strix uralensis: nuovi dati e quadro distributivo italiano. In S. G. Fasano & D. Rubolini (Eds.), *Riassunti del XIX Convegno Italiano di Ornitologia. Torino, 27 settembre - 1 ottobre 2017* (p. 38). Torino: Tichodroma. Monografie del Gruppo Piemontese Studi Ornitologici.

Roché, J. C., & Chevereau, J. (2000). *Une guide sonore des oiseaux d'Europe et du Maghreb*. Sittelle.

Rogers, T. L., Gouhier, T. C., & Kimbro, D. L. (2018). Temperature dependency of intraguild predation between native and invasive crabs. *Ecology*, *99*(4), 885–895. https://doi.org/10.1002/ecy.2157

Royle, J. A. (2004). N-Mixture Models for Estimating Population Size from Spatially Replicated Counts. *Biometrics*, *60*(1), 108–115. https://doi.org/10.1111/j.0006-

341X.2004.00142.x

Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, *1*(2), 103–113. https://doi.org/10.1111/j.2041-210X.2010.00012.x

Schweiger, O., Settele, J., Kudrna, O., Klotz, S., & Kühn, I. (2008). Climate change can cause spatial mismatch of trophically interacting species. *Ecology*, *89*(12), 3472–3479. https://doi.org/10.1890/07-1748.1

Scridel, D., Bogliani, G., Pedrini, P., Iemma, A., Von Hardenberg, A., & Brambilla, M. (2017). Thermal niche predicts recent changes in range size for bird species. *Climate Research*, *73*(3), 207–216. https://doi.org/10.3354/cr01477

Scully, A. E., Fisher, S., Miller, D. A. W., & Thornton, D. H. (2018). Influence of biotic interactions on the distribution of Canada lynx (Lynx canadensis) at the southern edge of their range. *Journal of Mammalogy*, *99*(4), 760–772. https://doi.org/10.1093/jmammal/gyy053

Sergio, F., Marchesi, L., Pedrini, P., & Penteriani, V. (2007). Coexistence of a generalist owl with its intraguild predator: distance-sensitive or habitat-mediated avoidance? *Animal Behaviour*, *74*(6), 1607–1616. https://doi.org/10.1016/j.anbehav.2006.10.022

Tjernberg, M., Johnsson, K., & Nilsson, S. G. (1993). Density variation and breeding success of the black woodpecker Dryocopus martius in relation to forest fragmentation. *Ornis Fennica*, *70*(3), 155–162.

Tylianakis, J. M., Didham, R. K., Bascompte, J., & Wardle, D. A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, *11*(12), 1351–1363. https://doi.org/10.1111/j.1461-0248.2008.01250.x

Valiente-Banuet, A., Aizen, M. A., Alcántara, J. M., Arroyo, J., Cocucci, A., Galetti, M., … Zamora, R. (2015). Beyond species loss: The extinction of ecological interactions in a changing world. *Functional Ecology*, *29*(3), 299–307. https://doi.org/10.1111/1365-2435.12356

Van der Putten, W. H., Macel, M., & Visser, M. E. (2010). Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *365*(1549), 2025–2034. https://doi.org/10.1098/rstb.2010.0037

Vos, C. C., Berry, P., Opdam, P., Baveco, H., Nijhof, B., O'Hanley, J., … Kuipers, H. (2008). Adapting landscapes to climate change: Examples of climate-proof ecosystem networks and priority adaptation zones. *Journal of Applied Ecology*, *45*(6), 1722–1731. https://doi.org/10.1111/j.1365-2664.2008.01569.x

Vrezec, A. (2009). Melanism and plumage variation in macroura Ural Owl. *Dutch Birding*, *31*, 159–170.

Vrezec, A. (2019). Kozača Strix uralensis. In T. Mihelič, P. Kmecl, K. Denac, U. Koce, A.

Vrezec, & D. Denac (Eds.), *Atlas ptic Slovenije. Popis gnezdilk 2002-2017* (pp. 214–215). Ljubljana: DOPPS.

Vrezec, A., & Bertoncelj, I. (2018). Territory monitoring of Tawny Owls *Strix aluco* using playback calls is a reliable population monitoring method. *Bird Study*, 1–11. https://doi.org/10.1080/00063657.2018.1522527

Vrezec, A., & Mihelič, T. (2013). The Ural Owl, Strix uralensis macroura, in Slovenia: an overview of current knowledge on species ecology. *Rivista Italiana Di Ornitologia*, Vol. 82, pp. 30–37. https://doi.org/10.4081/rio.2012.107

Vrezec, A., Saurola, P., Avotins, A., Kocijančič, S., & Sulkava, S. (2018). A comparative study of Ural Owl Strix uralensis breeding season diet within its European breeding range, derived from nest box monitoring schemes. *Bird Study*, *65*(sup1), S85–S95. https://doi.org/10.1080/00063657.2018.1553026

Vrezec, A., & Tome, D. (2004a). Altitudinal segregation between Ural Owl Strix uralensis and Tawny Owl S. aluco: Evidence for competitive exclusion in raptorial birds. *Bird Study*, Vol. 51, pp. 264–269. https://doi.org/10.1080/00063650409461362

Vrezec, A., & Tome, D. (2004b). Habitat selection and patterns of distribution in a hierarchic forest owl guild. *Ornis Fennica*, *81*(3), 109–118.

Wisz, M. S., Pottier, J., Kissling, W. D., Pellissier, L., Lenoir, J., Damgaard, C. F., … Svenning, J. C. (2013). The role of biotic interactions in shaping distributions and realised assemblages of species: Implications for species distribution modelling. *Biological Reviews*, *88*(1). https://doi.org/10.1111/j.1469-185X.2012.00235.x

Zielinski, W. J., Tucker, J. M., & Rennie, K. M. (2017). Niche overlap of competing carnivores across climatic gradients and the conservation implications of climate change at geographic range margins. *Biological Conservation*, *209*, 533–545. https://doi.org/10.1016/J.BIOCON.2017.03.016

Zink, R., & Walter, T. (2018). *Endbericht Habichtskauz Wiederansiedelung - 2015-2018*. Wien.

Zuur, A. F., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. https://doi.org/10.1007/978-0-387-87458-6